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Is the meiofauna a good indicator for climate change and anthropogenic impacts?

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Abstract Our planet is changing, and one of the most pressing challenges facing the scientific community revolves around understanding how ecological communities respond to global changes. From coastal to deep-sea ecosystems, ecologists are exploring new areas of research to find model organisms that help predict the future of life on our planet. Among the different categories of organisms, meiofauna offer several advantages for the study of marine benthic ecosystems. This paper reviews the advances in the study of meiofauna with regard to climate change and anthropogenic impacts. Four taxonomic groups are valuable for predicting

global changes: foraminifers (especially calcareous forms), nematodes, copepods and ostracods. Environmental variables are fundamental in the interpretation of meiofaunal patterns and multistressor experiments are more informative than single stressor ones, revealing complex ecological and biological interactions. Global change has a general negative effect on meiofauna, with important consequences on benthic food webs. However, some meiofaunal species can be favoured by the extreme conditions induced by global change, as they can exhibit remarkable physiological adaptations. This review highlights the need to incorporate studies on taxonomy,

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genetics and function of meiofaunal taxa into global change impact research.

Keywords Meiofauna · Climate change · Anthropogenic impacts · Biomonitoring · Natural observations and experimental studies

Introduction

The role of humans in altering the environment at a global scale is becoming increasingly evident (IPCC 2014); thus, it is crucial to understand the consequences of changes for life on Earth and human societies (Rudd 2014). In particular, the consequences of human actions on the environment need to be understood to mitigate their impacts. Since the effects will occur at a broad scale, understanding and attenuating potential global changes represents a tremendous scientific challenge.

The major global change that we are experiencing is linked to climate. Climate can be defined as the average weather in terms of the mean and its variability over a certain time span (Baede et al. 2001), while climate change can be defined as any systematic change in the climate system that is sustained over several decades or longer (Sijp et al. 2014). In the present study, we consider mainly the current climate change. Global surface warming has taken place at a rate of 0.74 ± 0.18 °C over the last 100 years (1906–2005) and the warming rate over the last 50 years is almost twice that of the entire 100-year period (IPCC 2007). Global warming itself expresses only one aspect of climate change. Global sea level rising, melting of ice sheets, and extreme weather events are other important aspects of climate change (Freedman 2014). Modelling studies predict that climate change over the next century will have profound consequences for marine biota, as well as for human populations living in coastal regions (Jones et al. 2013; Mora et al. 2013). With a constantly growing population and high energetic demands, human activities significantly affect ecosystems (Bampton 1999), and anthropogenic impacts are driving the observed changes (Barron 1989). Determining the ecological impact of humans on marine ecosystems requires a deep understanding of their interactions with these ecosystems (Kennedy and Jacoby 1999).

When compared with other ecosystem compartments included in models that aim at predicting and understanding global changes, meiofauna offer several advantages. Meiofauna is a collective name for one of the most diversified communities of the marine realm, including small organisms, unicellular protists and multicellular metazoans that live in aquatic sediments (Giere 2009; Fig. 1). Due to their high abundance and diversity, their widespread distribution, their rapid generation time and fast metabolic rates, meiofaunal organisms are vital contributors to ecosystem function, including nutrient cycling and the provision of energy to higher

trophic levels (Woodward 2010). These characteristics make meiofaunal organisms excellent candidates to test general ecological hypotheses and theories (Jessup et al. 2004; Nascimento et al. 2011, 2012; Bonaglia et al. 2014). However, this group represents an often neglected component of marine biodiversity (Curini-Galletti et al. 2012) and is generally poorly studied (particularly in the deep sea) because most applied programmes target the larger macrofauna, which are more readily identifiable and countable than meiofauna (Schratzberger et al. 2000).

To assess the general potential of meiofauna for predicting and assessing global change and other anthropogenic stressors, here we review advances in the study of meiofauna with regard to climate change and human impacts, preceded by a background session about the importance of meiofauna in marine benthic ecosystems. We conclude by suggesting perspectives and limits for the use of meiofauna as model organisms in future research related to global change.

Background

The term meiofauna (from the Greek μέγαν smaller) was coined in 1942 by Molly F. Mare “to define an assemblage of benthic metazoans that can be distinguished from macrofauna by their small sizes.” Considering the size boundaries (operationally defined based on the standardised mesh size of sieves with 1000 µm and 20 µm as upper and lower limits, respectively; Danovaro 2010), protists are also considered part of meiofauna (Giere 2009). Meiofauna represent the most diversified group in the marine realm, encompassing 24 of the 35 animal phyla, as well as one important group of protists, the foraminifera (Giere 2009). Meiofauna are mostly found in and on soft sediments, but also on and among epilithic plants and other types of substrata (e.g., animal tubes; Pinto et al. 2013). These small organisms can spend their complete life cycle without reaching sizes greater than 1 mm (permanent meiofauna), or be found in this size class for just a part of their life cycle (e.g., juveniles of macrofauna, referred to as temporary meiofauna; Hentschel and Jumars 1994). They are the most abundant size class in the benthos and are closely connected to other compartments of the benthos (including prokaryotes and macrofauna; Baldrighi et al. 2013). They play an important role in benthic food webs, not only as consumers (feeding on detritus, diatoms and algae, and preying on other small metazoans; Pergent et al. 1994; Duarte and Cebrian 1996; Gee and Somerfield 1997; Mateo and Romero 1997; Gwyther 2003; Torres-Pratts and Schizas 2007; Mascart et al. 2013, 2015), but also as producers (being a food source for macrofauna and fish; Gerlach 1978; Lebreton et al. 2011; Vinagre et al. 2012; Carpentier et al. 2014). The abundance, diversity, distribution and functional properties of meiofauna can be affected by several abiotic factors, including

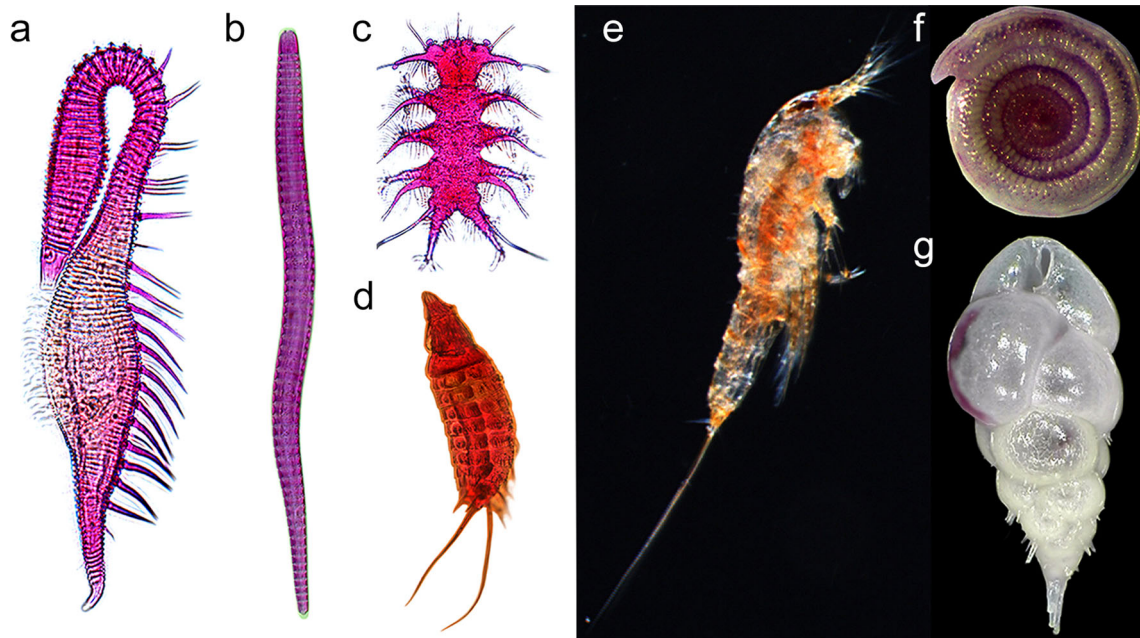


Fig. 1 Microscopic view of meiofauna. Representatives of selected meiofaunal taxa: **a, b**) Nematoda, **c**) Tardigrada, **d**) Kinorhyncha, **e**) Copepoda, **f, g**) Foraminifera. Credits: **a, b, c, d**: D. Zeppilli (IFREMER); **e**: Moorea Biocode project; **f**: C. Fontanier (IFREMER); **g**: Natural History Museum, London

temperature, salinity, hydrodynamic and sedimentary processes, sediment grain size, oxygenation level and food availability (Ingels et al. 2011; Lizhe et al. 2012; Ngo et al. 2013; Zeppilli et al. 2013; Górska et al. 2014; Pusceddu et al. 2014b), and also, by biotic factors such as predation and competition (Tita et al. 2000; Danovaro et al. 2007; Nascimento et al. 2011; Braeckman et al. 2013; Boldina et al. 2014). Meiofauna are characterised by a high sensitivity to environmental changes due to their short generation time and the lack of pelagic larval dispersion for the dominant meiofaunal groups (Bongers and Ferris 1999). Meiofauna can also modify their environments and promote the degradation of organic matter by stimulating microbial activity and bioturbating the sediment (Aller and Aller 1992; Giere 2009).

Marine meiofaunal diversity and ecosystem functioning

Ecosystem functions are considered as the sum of biological, geochemical, and physical processes that operate within an ecosystem, sustaining its overall performance and supplying ecosystem services (Edwards et al. 2014). Increased human pressure contributes to depauperate ecosystems, thereby potentially affecting their ability to provide essential services. The potential ecological consequences of biodiversity loss and the relationships between species diversity and ecosystem processes have aroused considerable interest in the scientific community (Loreau et al. 2001). It is now recognised that higher functional biodiversity contributes to a stable and resilient ecosystem (Tomimatsu et al. 2013). The marine environment covers a large majority (71 %) of the planet's surface,

shows high levels of diversity at all scales, and is essential to global fluxes of materials, nutrients, and energy to other ecosystems (Hooper et al. 2005). Understanding the relationship between diversity and stability is one of the major challenges in marine ecosystems ecology (Borja 2014), and the highly diverse meiofauna were only recently included in ecosystem functioning research. Several studies have shown that meiofaunal species richness has a positive effect on ecosystem functions (Covich et al. 2004). However, shallow-water soft-sediment studies show that species identity and function seems to be more important than species richness for the maintenance of ecosystem functioning (Radwell and Brown 2008). For example, in an experimental study, De Mesel et al. (2006) provide evidence for an idiosyncratic relationship between nematode species diversity and function in low-diversity systems. Furthermore, limited functional overlap between nematode species is observed in low diversity systems (De Mesel et al. 2006; Gingold et al. 2013). Using deep-sea nematodes as model organisms, Danovaro et al. (2008) suggest that high nematode diversity may have a positive impact on deep-sea ecosystem functioning. This exponential diversity-function relationship may only apply to low diversity assemblages due to increased competition or greater functional redundancy in more diverse assemblages (Leduc et al. 2013). Although the positive relationship between diversity and ecosystem functioning is well defined when nematode species diversity is low in deep-sea ecosystems, the correlation is absent when species diversity is high (Leduc et al. 2013). This may explain why in the South Pacific, the relationship between diversity and ecosystem functioning appears weaker, whereas in other regions,

such as the Atlantic Ocean and Mediterranean Sea, the relationship is stronger (Leduc et al. 2013). On the continental slope of the northwestern Mediterranean Sea, deep-sea fisheries have caused the collapse of benthic meiofaunal biodiversity and ecosystem functioning, with potential consequences on biogeochemical cycles (Pusceddu et al. 2014a). Moreover, a recent study assessed the influence of meiofauna on the relationship between macrofaunal biodiversity and ecosystem functioning (Piot et al. 2014), highlighting the fact that meiofauna may have a strong direct impact on benthic properties, by modifying the interactions between macrofaunal species, and therefore their impacts on ecosystem properties.

The ecological role of meiofauna in benthic ecosystems can be assessed by measuring the flow of energy. Small organisms are characterised by high dynamics (oxygen consumption and metabolism) and turnover (Gerlach 1971). Compared with macrofauna, meiofauna usually have low standing stock biomass, but high production (Giere 2009). In some shallow ecosystems, such as tidal flats, meiofaunal secondary production frequently exceeds that of macrofauna (Warwick et al. 1979; Kuipers et al. 1981). Small benthos, including meiofauna, clearly contribute substantially to production in sandy sublittoral ecosystems: up to 40 % of the total benthic metabolism (Fenchel 1978). Generally, the biomass and organic matter cycling by small heterotrophs (meiofauna and bacteria) increase in importance with depth when resources are limited (Heip et al. 2001; Thistle 2001; Rowe et al. 2003; Baguley et al. 2005; Rex et al. 2006; Gontikaki et al. 2011). The depiction of meiofauna in energy flux diagrams suffers from a lack of ecological information for many constituent taxa (Giere 2009). The central role of detritus in the meiofaunal energy budget (Escaravage et al. 1989) derives from the consumption of detritus and microorganisms by the most abundant meiofaunal groups, nematodes and foraminifera (Gooday 2003; Murray 2006). Grazing meiofauna stimulate microbial activity by keeping the microbial population in its reproductive log-phase (Giere 2009). Many studies show that meiofauna feed on benthic microalgae, freshly sedimented phytodetritus and seagrass detritus (Lee 1980; Rudnick 1989; Riera et al. 1996; Olafsson and Elmgren 1997; Buffan-Dubau and Carman 2000; Gooday 2003; Murray 2006; Torres-Pratts and Schizas 2007; Mascart et al. 2013, 2015). Nematode responses to food availability as well as to other environmental factors can be species-specific with a complex relationship between species diversity and function (Dos Santos et al. 2008). Meiofauna represent, in turn, an important food resource for macrofauna and a variety of juvenile fish (Giere 2009). In situ and laboratory experiments give fairly accurate information on the role of foraminifera in the food web and energy transfer within benthic environments (e.g., Nomaki et al. 2005a, 2005b, 2006, 2009, 2010, 2011; Würzberg et al. 2011). Oxygen consumption rates in meiofaunal organisms are greater than in macrofaunal

organisms (Mahaut et al. 1995). Meiofauna may be five times more metabolically active than macrofauna, consuming between 200 and 2000 mm³ O₂/h/g wet weight compared to 200 to 500 mm³ O₂/h/g wet weight for macrofauna in sublittoral sediments (Gerlach 1971). In the deep sea, the respiration rate of meiofauna increases with depth, whereas it decreases in larger organisms (Mahaut et al. 1995). For instance, deep-sea foraminifera (e.g., *Uvigerina semiornata*) from the Indo-Pakistan oxygen minimum zone (OMZ) dominate the uptake of fresh organic matter when bottom-water oxygenation is very low (~5 mmol/L), whereas larger metazoans (polychaetes) are more efficient in food acquisition when oxygenation is higher (Woulds et al. 2007). Furthermore, benthic foraminifera are capable of denitrification as an alternative metabolic pathway (Risgaard-Petersen et al. 2006; Piña-Ochoa et al. 2010a, b).

Global climate change

Climate change, caused by an increase in atmospheric carbon dioxide (CO₂) over the past centuries, has already caused significant shifts in marine and terrestrial ecosystems (Ingels et al. 2012). The direct consequences of increasing CO₂ include the increase in ocean temperature (Bindoff et al. 2007) and acidity (Doney et al. 2009). The ocean temperature is warming (the upper 75 m of seawater has warmed by 0.11 °C per decade from 1971 to 2010), the sea level is rising (global mean sea level has risen by 0.19 m during the 1901–2010 period) and sea surface salinity has increased by 0.13 PSS78 (Practical Salinity Scale 1978) from 1950 to 2008 (Durack and Wijffels 2010). CO₂ concentrations in the atmosphere have increased up to 40 % since pre-industrial times, primarily due to fossil fuel combustion and carbon emissions from land (IPCC 2014). Historically, the oceans absorbed approximately one-quarter of all CO₂ released into the atmosphere, resulting in a 26 % increase in the acidity of the ocean (IPCC 2014). Over the last four decades, the extent of hypoxic zones and OMZs has significantly increased (Diaz and Rosenberg 1995; Rabalais et al. 2010; Stramma et al. 2008, 2010). Other changes may occur in ocean stratification and circulation (Doney et al. 2012). Climate change probably affects the number of hurricanes and causes changes in current systems, leading to the mass destruction of habitats. The speed of the current climate change is comparable with other dramatic episodes in our planet's history that led to mass extinction events (Van De Schootbrugge and Gollner 2013).

Modelling studies predict global changes in ocean temperature, pH, oxygenation and primary production over the next century, with profound potential consequences for marine biota in general, as well as for human populations living in coastal regions (Jones et al. 2013; Mora et al. 2013). The effects of climate change are particularly evident in the Arctic

Ocean and some parts of the Antarctic Ocean (Doney et al. 2012). In the latter, the low sea-surface temperature, leading to increased CO₂ solubility and upwelling of rich CO₂ deep water, has led to rapid acidification rates (Guinotte and Fabry 2008). In the Southern Hemisphere, the Antarctic Peninsula is experiencing one of the fastest rates of regional climate change on Earth (Turner et al. 2009) and Antarctic ecosystems are particularly vulnerable and sensitive to these changes (Ingels et al. 2012). Global climate warming also has secondary effects, such as large-scale ice-shelf disintegration events, changes in the availability, quantity and quality of food, and increased glacier melting leading to increased coastal turbidity and salinity modifications (Ingels et al. 2012). A summary of studies concerning the impact of climate change on marine meiofauna is reported in Tables 1 and 2.

Impact of global climate change on meiofauna

Response to ocean warming

Recent studies have shown that meiofaunal communities respond to warming both in seawater and freshwater ecosystems (O’Gorman et al. 2012; Gingold et al. 2013). In freshwaters, macrofaunal and meio community composition has been shown to change dramatically across a thermal gradient, with indications of low food-web stability in warmer currents (O’Gorman et al. 2012). In subtropical meiofaunal communities, an increase of temperature negatively affects species-rich communities, causing the mortality of dominant species, which may have serious consequences for the benthic food web (Gingold et al. 2013). In the deep eastern Mediterranean Sea, global warming has altered the carbon and nitrogen cycles and has had negative effects on deep-sea bacteria and benthic meiofauna in terms of abundance and diversity (Danovaro et al. 2004a). Furthermore, deep-sea meiofaunal secondary production is expected to decrease in many parts of the ocean due to ocean warming (Smith et al. 2008; Mora et al. 2013).

An experimentally induced warming of 4 °C in coastal sediments showed that heterotrophic variables (bacterial production, meiofaunal biomass, and fluxes of oxygen) respond more clearly to warming than do autotrophic variables (oxygen production, nutrient uptake, and total alkalinity; Alsterberg et al. 2011). Another in situ experiment showed that global warming has also altered body-size population structure, resulting in a disruption in top-down control, whereas eutrophication embodies changes in bottom-up forcing (Jochum et al. 2012). In another mesocosm experiment, the reduction in top-predator body mass enabled the development of a greater intermediate fish predator biomass, and in turn, suppressed key micrograzers (mainly meiofaunal copepods), which led to an overall increase in microalgal biomass (Jochum et al. 2012). Even so, results coming from short-

term mesocosm experiments have to be interpreted cautiously, considering that climate change takes place over much longer time scales than ecological mechanisms might compensate for. Several culture experiments showed the strict relationship between temperature and nematode life cycles (e.g., Gerlach and Schrage 1971; Hopper et al. 1973; Warwick 1981b). In general, life cycles become shorter with increased temperature (Gerlach and Schrage 1971; Hopper et al. 1973), and in some cases at low temperatures, nematodes can shift to a vivipary reproduction mode (Gerlach and Schrage 1971). Moens and Vincx (2000) investigated the influence of salinity and temperature on the life history of two estuarine nematode species. They showed that temperature significantly influenced both nematode species, while salinity had relatively minor effects on fecundity and development times, but strongly impacted juvenile viability at the end of the salinity range (0 and 40‰; Moens and Vincx 2000). Furthermore, larger benthic foraminifera (e.g., *Amphistegina*, *Heterostegina*), hosting endosymbiotic algae, suffer remarkable bleaching (symbiont or pigment loss) due to temperature-induced stress in culture experiments (e.g., Talge and Hallock 2003; Schmidt et al. 2011).

Response to ocean acidification

A number of acidification experiments (ex situ and in situ) focusing on meiofauna compartment have been conducted on shallow-water and deep-sea benthic ecosystems (e.g., Barry et al. 2004; Thistle et al. 2006; Ricketts et al. 2009; Fleeger et al. 2010; McIntyre-Wressnig et al. 2013). The intensity of response varies with the distance and intensity of the acidification source (Ricketts et al. 2009). In general, an increase in mortality, combined with a decrease in species richness, is observed (Thistle et al. 2006). In coral reefs, coral bleaching caused by high temperature and increasing acidity led to the replacement of coral reefs by algae and favoured the development of meiofaunal communities on dead corals (Hoegh-Guldberg et al. 2007). In an experimental mesocosm, acidification led to changes in nematode communities in sediments affected by burrowing urchins (Dashfield et al. 2008). Another experiment proved that acidification had a significant impact on the structure and diversity of nematode communities, especially in sandy sediment nematofauna (Widdicombe et al. 2009). On the other hand, a 56-day CO₂ enrichment in a coastal microcosm caused no significant differences in the abundance of total meiofauna (nematodes and harpacticoid copepods; Kurihara et al. 2007). Similarly, fitness and survival of larger benthic foraminifera sampled from reefs were not directly affected by increased partial pressure of CO₂ and the concomitant decrease in pH and calcite saturation states. Nevertheless, a range of non-lethal effects, including partial test dissolution and symbiont loss, was observed (McIntyre-Wressnig et al. 2013), and several studies have reported the dissolution of calcareous foraminiferal tests in low pH

Table 1 A summary of meiofauna studies reported in the “Global climate change” session

Domain	Kind of observation	Habitat and geographic coverage	Taxa investigated	Response	Reference
Ocean warming	Shallow water	Gulf of California, Mexico	Nematoda	High diversity: negative response; low diversity: idiosyncratic response	Gingold et al. 2013
	Shallow water	Munkeby Bay, Sweden	Meiofaunal and bacterial biomass	Heterotrophic variables (e.g., meiofaunal biomass) respond clearly than autotrophic variables	Alsterberg et al. 2011
	Shallow water	Conch and Tennessee Reefs, Florida	Foraminifera	Foraminifera with symbionts experience bleaching	Talge and Hallock 2003
	Shallow water	Great Barrier Reef Marine Park, Australia	Foraminifera	Foraminifera with symbionts experience bleaching	Schmidt et al. 2011
	Shallow water	Helgoland, North Sea	Nematoda	Nematode life cycles become shorter with increased temperature	Gerlach and Schrage 1971
	Shallow water	Magueyes Island, Puerto Rico	Nematoda	Nematode life cycles become shorter with increased temperature	Hopper et al. 1973
	Shallow water	Lynher Estuary, UK	Nematoda	Nematode life cycles become shorter with increased temperature	Warwick 1981b
	Shallow water	Westerschelde Estuary, the Netherlands	Nematoda	Nematode life cycles become shorter with increased temperature	Moens and Vincx 2000
	Deep sea	Natural observation	Nematoda	Negative response	Danovaro et al. 2004a
	Shallow water	Laboratory experiment	Nematoda and Copepoda	No response	Kurihara et al. 2007
Ocean acidification	Shallow water	Laboratory experiment	Foraminifera	Dissolution of tests and loss of symbionts	McIntyre-Wressnig et al. 2013
	Shallow water	Mesocosm experiment	Nematoda	Impacts on structure and diversity of nematode community	Dashfield et al. 2008
	Shallow water	Mesocosm experiment	Meiofauna and Macrofauna	Impacts on structure and diversity of nematode community	Widdicombe et al. 2009
	Shallow water	Mesocosm experiment	Meiofauna and Macrofauna	Impact macrofauna negatively whereas nematode abundance and diversity increase	Hale et al. 2011
	Deep sea	In situ experiment	Meiofauna	Meiofaunal mortality, increase in nematode abundance	Barry et al. 2004; Carnan et al. 2004; Thistle et al. 2005, 2007
	Deep sea	In situ experiment	Copepoda	General increase in mortality and decrease in species richness	Thistle et al. 2006
	Deep sea	In situ experiment	Foraminifera	Decrease in abundance and diversity, increase of non-calcareous forms	Ricketts et al. 2009
	Deep sea	Modeling	Meiofauna, Macrofauna and Megafauna	Decrease in meiofaunal biomass	Jones et al. 2013
	Deep sea	Review study	Foraminifera, Nematoda, Amphipoda, Isopoda, Echinoidea	Deep-sea ecosystems: changes in foraminiferal community affects isopods and scaphopods	Ingels et al. 2012
		Review study	Meiofauna		Giere 1993

Table 1 (continued)

Domain	Kind of observation	Habitat and geographic coverage	Taxa investigated	Response	Reference
Ocean warming and acidification Hypoxic environments	Several studies/ domains			Meiofauna tolerate low oxygen concentrations better than macrofauna	
	Shallow water	Louisiana Coast	Meiofauna	Decrease in meiofaunal abundance and diversity	Murell and Fleeger 1989
	Shallow water	Crimean shores of the Black Sea	Meiofauna	Changes in meiofaunal composition	Revkov and Sergeeva 2004
	Shallow water	Adriatic Sea, Mediterranean Sea	Copepoda	Anoxia impacts the survival of consumers and also of primary producers with important implications for the recovery phase	De Troch et al. 2013
Shallow water	In situ experiment	Adriatic Sea, Mediterranean Sea	Meiofauna	Induced hypoxic/anoxic disturbance meiobenthic communities appear highly resilient	Guerrini et al. 1998
	Microcosm Experiment	Baltic Sea	Meiofauna and Macrofauna	The ostracod species <i>Heterocypridis sorbyana</i> and <i>Candona neglecta</i> , the group Kinorhyncha, the nematode species <i>Leptolaimus elengans</i> , <i>L. papilliger</i> and <i>Sabatieria pulchra</i> are tolerant to hypoxic conditions	Modig and Olafsson 1998
	Laboratory experiment	Adriatic Sea, Mediterranean Sea	Copepoda	Copepoda belonging to the family Cletodidae tolerate anoxia	Grego et al. 2013
	Laboratory experiment	Westerschelde Estuary, the Netherlands	Meiofauna and Macrofauna	Hypoxia changed nematode community composition (<i>Odontophora</i> tolerant genus)	Van Colen et al. 2009
Epipelagic	Natural observation	Gulf of Tehuantepec, Mexico	Foraminifera	Complete mortality, as for macrofauna, did not occur	Perez-Cruz and Machain-Castillo 1990
	Natural observation	Black Sea	Meiofauna	Foraminifera exhibit a thinner and more porous shell	Sergeeva and Zaika 2013
	Natural observation	Volcano 7 Seamount, Eastern Tropical Pacific	Bacteria, Meiofauna, Macrofauna, Megafauna	Nematodes are generally more resistant to hypoxia than copepods	Levin et al. 1991
	Natural observation			Bacteria and meiofauna attained peak abundances on the low-oxygen upper summit, however, copepods were greatly reduced by oxygen limitation	
Deep sea	Natural observation	Oman slope, Arabian Sea	Nematoda	Food quality rather than oxygen was the major predictor of nematode abundance	Cook et al. 2000
	Natural observation	Oman slope, Arabian Sea	Foraminifera	Soft-shelled monothalamous taxa rare and large agglutinated taxa absent in the most oxygen-depleted sites	Goody et al. 2000
	Review study	Eastern Pacific Ocean, off west Africa and in the Arabian Sea and Bay of Bengal	Meiofauna	Meiofauna (Foraminifera and Nematoda) dominate OMZs at an O ₂ concentration of <0.1 mL/L	Levin 2003

Table 1 (continued)

Domain	Kind of observation	Habitat and geographic coverage	Taxa investigated	Response	Reference
Several studies/ Domains	Review study	Several studies/sites	Foraminifera	Small thin-walled species are common, but forms with larger pores may be present	Sen Gupta and Machain-Castillo 1993
Sea level modifications	Natural observation	The Humber Estuary, the Ythan Estuary and the Firth of Forth, UK	Meiofauna and Macrofauna	Decrease in meiofaunal abundance	Yamanaka et al. 2010
Sea surface primary production	Review study	Several studies/sites	Bacteria, Meiofauna, Macrofauna, Megafauna	Ecosystem structure and function in the abyss are strongly modulated by the quantity and quality of detrital food material sinking from the surface ocean	Smith et al. 2008
Episodic events	Natural observation	East–northwest transect off Central Chile	Meiofauna	El Niño negatively affects meiofaunal abundance, copepods are positively affected	Neira et al. 2001
Deep sea	Natural observation	Adriatic Sea, Mediterranean Sea	Meiofauna	DSWC negatively affects meiofaunal abundance, biomass and diversity	Pusceddu et al. 2013
Ice-shelf modifications	Natural observation	Ikka Fjord, Greenland, Arctic	Meiofauna	Threat of loss of endemic meiofauna of NOW-/NEW-polynyas and of Ikka fjord	Huys et al. 1997; Worsaae and Kristensen 2003; Sørensen and Kristensen 2000
Shallow water	Natural observation	Potter Cove, King George Island (South Shetland Islands)	Microbenthos, meiofauna and macrofauna	Low densities of meiofauna in recently ice-free areas, but high abundance of the pioneer genus <i>Microloaimus</i>	Pasotti et al. 2014
Mesopelagic	Natural observation	Larsen area, Antarctic Peninsula	Nematoda	Increase in nematode abundance and biomass due to phytoplanktonic blooms	Raes et al. 2010
Mesopelagic	Natural observation	Larsen area, Antarctic Peninsula	Meiofauna, Macrofauna and Megafauna	Impoverishment of meiofauna	Gutt et al. 2011

Table 2 A summary of meiofauna studies reported in the “Other anthropogenic impacts” session

Domain	Kind of observation	Habitat and geographic coverage	Taxa investigated	Response	Reference
Trawling/ physical disturbances	Shallow water	North and Irish Sea	Nematoda	Nematodes are affected by intense trawling on muddy fishing grounds	Hinz et al. 2008
	Shallow water	Thermaikos Gulf, Northern Aegean Sea, Mediterranean Sea	Meiofauna	No short term trawling impacts on meiofauna abundance and community structure	Lampadariou et al. 2005
	Shallow water	Hamilton harbour	Meiofauna and Macrofauna	Meiofauna were less affected than macrofauna by physical disturbance of the sediment by the passage of large cruise liners	Warwick et al. 1990
	Shallow water	Port Shelter, Hong Kong Island, China	Nematoda	Positive response	Liu et al. 2009
	Shallow water	Venice Lagoon, NW Adriatic Sea, Mediterranean Sea	Meiofauna and Macrofauna	Modification in macrofauna immediately after the disturbance, meiofauna calings recorded after 1 week	Pranovi et al. 2000
Industrial discharge of hydrocarbons	Shallow water	Southern North Sea	Meiofauna	No short- to medium-term trawling impacts on meiofaunal diversity and biomass. Effects on community structure	Schratzberger et al. 2002
	Shallow water	Southwest England	Nematoda	Sand nematodes suffered when exposed to organic enrichment, mud nematodes are more sensible to physical disturbance	Schratzberger and Warwick 1998a, 1999
	Shallow water	Oslofjord, Norway	Nematoda	Removal of larger macrofauna as a result of trawling increase nematode abundance	Ingels et al. 2014
	Deep sea	La Fonera Canyon, Mediterranean Sea	Meiofauna	Negative response	Puscaddu et al. 2014a
	Shallow water	Taeon coast, Yellow Sea, Korea	Meiofauna	Oil spill experiment: dramatic impoverishment of meiofaunal abundance during the first 4 days after the contamination with slow recover (up to 1 month)	Kang et al. 2014
	Shallow water	Tunisian lagoon	Nematoda	Some nematode species (e.g., <i>Oncholaimus campylocercoides</i> and <i>Chaetonema sp.</i>) are negatively affected while others (e.g., <i>Marfylinia stekhoveni</i>) are positively affected	Mahmoudi et al. 2005
	Shallow water	Bay of Bourgneuf, France	Foraminifera	Changes in foraminifera community	Ernst et al. 2006
	Shallow water	Tunisian lagoon	Nematoda	<i>Spirinia parastifera</i> became the dominant species (70 % relative abundance) and appeared to be an “opportunistic” species to PAH contamination while <i>Oncholaimus campylocercoides</i> and <i>Neochromadora peoclosoma</i> were strongly inhibited.	Louati et al. 2014
	Deep sea	Gulf of Mexico	Meiofauna	Reduction of meiofaunal diversity. Increase of nematodes near the oil spill	Montagna et al. 2013
	Deep sea	Gulf of Mexico	Nematoda	Changes in nematode community with increase of predators/scavengers	Bik et al. 2012b
Thermal pollution	Shallow water	North Port, New York	Benthic fauna	Decrease in diversity, changes in community, disappearance of sensitive species	Hechtel et al. 1970
	Shallow water	Hadera power plant, Israel	Foraminifera	Negative effect	Arel et al. 2011
	Shallow water	Lancashire, UK	Nematoda	High temperature increased nematode ingestion rates, while longevity decreased	Woombs and Laybournparry 1984a, b
Algal blooms due to agriculture discharge	Shallow water	Seagrass beds, Moreton Bay, Australia	Meiofauna	Phytoplankton blooms: changes in abundance and vertical profile of nematodes and copepods	Garcia and Johnstone 2006
	Shallow water	Venice Lagoon, Adriatic Sea, Mediterranean Sea	Meiofauna	Green algae blooms: changes in nematode community	Villano and Warwick 1995
	Shallow water	Brittany coasts, France	Meiofauna	Green algae blooms: decrease in meiofaunal abundance and diversity changes in nematode community	Carriço et al. 2013
	Shallow water	Wadden Sea of Lower Saxony	Meiofauna		Neira and Rackemann 1996

Table 2 (continued)

Domain	Kind of observation	Habitat and geographic coverage	Taxa investigated	Response	Reference
Sewage	Shallow water	Several studies/sites	Meiofauna	Green algae blooms: the changed chemical conditions in the sediment resulted in long and drastic reductions in meiofaunal abundance and number of taxa	Giere 2009
	Shallow water	Kiel fjord, Germany; the Garroch Head sewage-sludge dump ground in the Firth of Clyde, Scotland; Cornelian Bay, N.E. England; the Tyne Estuary, N.E. England; Sete, N.W. Mediterranean, France; Blanes Bay, N.W. Mediterranean, Spain	Nematoda	Phytoplankton blooms: increase in abundance and diversity	Warwick and Robinson 2000
	Shallow water	In situ experiment	Nematoda	Species of the marine nematode genus <i>Pontonema</i> dominate the macrobenthos under abnormally high conditions of particulate organic enrichment	
	Shallow water	Transplantation experiment	Nematoda		
Heavy metals	Shallow water	Hong Kong Island, China	Nematoda	Green algae blooms: dominance of <i>Sabatieria pulchra</i>	Wetzel et al. 2002
	Shallow water	Cienfuegos Bay, Cuba, Caribbean Sea	Nematoda	Nematode community composition in the sewage polluted sediments required longer time for recovery than nematode community from not polluted sediments	Liu et al. 2011
	Shallow water	Microcosm experiment	Nematoda	Changes in nematode community: increase of <i>Daptonema</i> , <i>Sabatieria</i> , <i>Pontonema</i> and <i>Linhomoeidae</i>	Armenteros et al. 2010
	Shallow water	Laboratory experiment	Nematoda	Nematodes tolerate osmotic stress regulating their water content with morphology and cuticular changes	Forster 1998
	Shallow water	Natural observation	Nematoda	Coloniser genera, as <i>Monhystera</i> and <i>Theristus</i> dominated the most polluted sites	Gyedu-Ababio and Baird 2006
	Shallow water	Natural observation	Foraminifera	<i>Ammonia tepida</i> exhibits high resistance to heavy metals	Ferraro et al. 2006
	Shallow water	Microcosm experiment	Meiofauna	Nematodes are not sensitive to TBT-contaminated as other infaunal benthos	Austen and McEvoy 1997
	Shallow water	Microcosm experiment	Nematoda	Impact on the nematode density, diversity, and community structure. <i>Axonolaimus</i> , <i>Theristus</i> , and <i>Paramonohystera</i>	Gyedu-Ababio et al. 1999
	Shallow water	Laboratory experiment	Nematoda	The metal taken up is associated with the cuticle and with a group of tissues including the hypodermis	Howell 1983
	Shallow water	Laboratory experiment	Nematoda	<i>Diploelasma</i> exhibits high resistance to heavy metals	Vranken and Heip 1986
Aquaculture	Shallow water	Ostende, North Sea	Nematoda	<i>Monhystera disjuncta</i> exhibits high resistance to heavy metals	Vranken et al. 1991
	Shallow water	Yeu Island, Atlantic Ocean	Foraminifera	Foraminifera experience test deformities and modifications in community structure	Le Cadre and Debenay 2006
	Shallow water	Natural observation	Meiofauna	Meiofauna under the cages are characterised by increased importance of polychaetes and copepods in comparison with a much lower importance of gastropods and kinorhynchids	Mirto et al. 2012
	Shallow water	Natural observation	Foraminifera	Foraminifera decrease or disappear	Schafer et al. 1995
	Shallow water	Natural observation	Foraminifera	Foraminifera decrease or disappear	Angel et al. 2000; Oron et al. 2014
	Shallow water	Natural observation	Foraminifera	Foraminifera decrease or disappear	Vidovic et al. 2009

Table 2 (continued)

Domain	Kind of observation	Habitat and geographic coverage	Taxa investigated	Response	Reference
Shallow water	Natural observation	Southern Brazil	Nematoda	The number of nematode genera, diversity, dominance and trophic diversity were significantly lower under the mussel farms than at the control sites	Netto and Valgas 2010
Shallow water	Natural observation	Adriatic Sea, Mediterranean Sea	Copepoda	Copepoda decrease and change in community structure	Grego et al. 2009
Shallow water	Microcosm experiment	Southwest England	Nematoda	Small doses of organic matter had milder effect on nematode community structure than the same quantity distributed fewer times, but in larger doses	Schratzberger and Warwick 1998b
Dumping of dredged material	Natural observation	Titchmarsh Marina, Essex, UK	Meiofauna and Macrofauna	Macrofaunal and meiofaunal communities from impacted sites are significantly different from those from nonimpacted sediments	Bolam et al. 2006
Alien species	Natural observation	NW Mediterranean	Meiofauna	Changes in community structure after invasion of <i>O. ovata</i>	Guidi-Guilvard et al. 2012
Shallow water	Natural observation	North Sea	Foraminifera	Invasion of alien species of Foraminifera	Gollasch 2002
Shallow water	Natural observation	Marenes-Oléron bay and Ile de Ré, Atlantic Ocean	Foraminifera	Invasion of alien species of Foraminifera	Bouchet et al. 2007
Shallow water	Natural observation	Indian ocean / North Sea	Copepoda	Invasion of alien species of Copepoda	Gollasch et al. 2000
Shallow water	Natural observation	Canadian Pacific coasts	Copepoda	Invasion of alien species of Copepoda	Levings et al. 2004
Shallow water	Natural observation	Baltic Sea	Meiofauna	Decrease in meiofaunal abundance and diversity. Tolerant nematode genera: <i>Subutieria</i> , <i>Terschellingia</i> , <i>Halomonhystera</i> .	Grzelak and Kotwicki 2014
Nuclear wastes	Natural observation	Novaya Zemlya Archipelago, Barents and Kara Seas	Meiofauna	Halomonhystera with ovoidiparus reproduction	Galtsova et al. 2004
Shallow and deep waters	Review study	Russian Arctic shelf	Meiofauna	Increase in diversity	Alexeev and Galtsova 2012
Deep sea	Natural observation	Novaya Zemlya in the Russian Arctic	Meiofauna	Changes in meiofaunal community	Pogrebov et al. 1997
Shallow water	Natural observation	Fal Estuary system, Cornwall, UK	Meiofauna	Mining wastes: some nematode species may develop different tolerance mechanisms	Somerfield et al. 1994
Shallow water	Micro/Mesocosm experiments	Sumbawa, Indonesia	Meiofauna	Mining wastes, micro/mesocosm experiment: meiofauna colonised tailing sediments after 40 days and recovered control values after 97 day.	Gwyther et al. 2009
Deep sea	Natural observation	Pacific Ocean	Meiofauna	Threat of loss of endemic nodule meiofauna	Bussau 1992; Bussau 1993; Thiel et al. 1993; Bussau et al. 1995;
Deep sea	Natural observation	Pacific Ocean	Nematoda	Negative impact on nematode abundance and diversity 26 years after disturbance	Veillette et al. 2007a, b
Deep sea	Review study	Several studies/sites	Meiofauna	Negative impact on nematode and copepod abundance and diversity	Miljuin et al. 2011 Radziejewska 2014

sediments (Green et al. 1993; Mojtabid et al. 2008). In a mesocosm experiment, which combined acidification and warming of the water, the abundance and diversity of macrofauna were negatively affected, while the abundance of nematodes increased due to the reduction in predation and competition (Hale et al. 2011).

Deep-sea sedimentary organisms are expected to be more sensitive to perturbations than are shallow-water ones, because natural deep-sea CO₂ concentrations and pH are less variable than in shallow water (Fleeger et al. 2010). Changes in foraminiferal assemblages due to acidification may have consequences for specialist predators, such as certain isopods and many scaphopods (Ingels et al. 2012). A series of in situ experiments at 3600 m off the coast of Monterey Bay (California) were performed by releasing small pools of liquid CO₂ to evaluate the potential impacts of a large scale deep-sea carbon dioxide storage program on benthic deep-sea communities (Barry et al. 2013). The results showed that meiofauna experienced high mortalities after exposure to episodic pH changes (Barry et al. 2004; Carman et al. 2004; Thistle et al. 2005, 2006, 2007). These changes may lead to a decline in meiofaunal biomass, although the decrease is likely to be less than that for larger size classes (macrofauna and megafauna; Jones et al. 2013). These experiments also showed the dissolution of calcareous foraminiferal tests leading to a decrease in the total number of foraminifera and species richness and an increase in the relative abundance of non-calcareous (agglutinated) forms (Ricketts et al. 2009).

Response to ocean deoxygenation

Because oxygen solubility is inversely correlated with temperature, global warming is already leading to a reduction in oceanic oxygen concentrations (Matear and Hirst 2003). Global warming intensifies hypoxia in OMZs and leads to geographical expansion of existing OMZs; for example, in the eastern Pacific and the Arabian Sea (Stramma et al. 2012). An increase in the number of OMZs is expected in the future (Stramma et al. 2012). In deeper waters, naturally occurring OMZs are located mainly in the eastern Pacific, the Arabian Sea and the Bay of Bengal (Helly and Levin 2004), and they harbour organisms that are adapted to low levels of oxygen.

Prolonged exposure to hypoxic conditions affects the entire meiofaunal community (Wetzel et al. 2001; Sergeeva and Zaika 2013). Meiofauna appear to better tolerate low concentrations of oxygen than macrofauna (Giere 1993). In the core OMZ regions, where oxygen concentrations typically drop below 0.1 mL/L, the fauna is primarily made up of small organisms, dominated by foraminifera and nematodes (Levin et al. 1991; Levin 2003; Gooday et al. 2009b), while macrofaunal organisms are rare or absent (Levin et al. 1991; Gooday et al. 2000, 2009a, 2009b; Levin 2003). Behavioural (escape,

predation reduction) and physiological responses (growth rate decrease, dormancy, initiation of anaerobic metabolism) to hypoxic conditions have been recorded in meiofauna (Rabalais et al. 2002), with a general decrease in meiofaunal densities due by the disappearance of many species (Diaz and Rosenberg 1995). This trend was also noticed in the Gulf of Mexico, where a dramatic decrease in meiofaunal abundance and biomass was detected in association with hypoxia and anoxia events (Murrell and Fleeger 1989). Furthermore, meiofaunal composition can modify according to changes in the hypoxic zone (Revkov and Sergeeva 2004). However, in an OMZ on the Oman slope (Arabian Sea), Cook et al. (2000) showed that food quality rather than oxygen was the major predictor of nematode abundance, highlighting the importance of ecological conditions in hypoxic environments.

In situ experiments confirm natural observations: hypoxia caused a dramatic collapse of the macrofaunal community, while meiofauna survived (Van Colen et al. 2009). Responses to stress vary depending on the species as well as the duration, severity, and frequency of the hypoxic periods (De Troch et al. 2013). In a short incubation time experimental setting, total meiofaunal density was not affected by anoxic conditions, due to the dominance of highly tolerant nematodes (De Troch et al. 2013). In another experimental study on Westerschelde Estuary tidal flats (The Netherlands), hypoxia caused a dramatic change in nematode community composition, with reduced diversity and abundance of all dominant nematodes, except for *Odontophora* spp. (Van Colen et al. 2009). A field experiment carried out in the Northern Adriatic Sea lagoon showed that nematodes were particularly resistant to the induced hypoxic/anoxic disturbance (Guerrini et al. 1998).

Nematodes are adapted to extreme environments through detoxification strategies and high anaerobic capacity (Veit-Köhler et al. 2009; Vopel et al. 1998). As such, they can be used to detect changes in oxygen levels in marine environments. Harpacticoid copepods are the most sensitive meiofauna taxa to low oxygen concentrations (De Troch et al. 2013). Several studies have shown that nematodes are generally more resistant to hypoxia than copepods (Murrell and Fleeger 1989; Modig and Olafsson 1998; Grego et al. 2013; Sergeeva and Zaika 2013). Copepods may stop feeding under anoxic conditions, yielding increased primary producer levels (De Troch et al. 2013). Nevertheless, some eucalanid copepods have a reduced aerobic metabolism that allows them to live permanently in OMZs (Teuber et al. 2013), and some species such as *Calanus chilensis* show high values of lactate dehydrogenases, which help their transit through OMZs during their daily migration (Teuber et al. 2013). In response to hypoxia, calcareous foraminifera optimise their oxygen capture by becoming smaller (Bernhard and Sen Gupta 1999; Levin 2003), and exhibiting a thinner and more porous shell (Bradshaw 1961; Phleger and Soutar 1973; Perez-Cruz and Machain-Castillo 1990; Sen Gupta and Machain-Castillo

1993; Gooday et al. 2000). These morphological changes improve oxygen exchange, but make them even more vulnerable to dissolution in the low pH conditions that prevail in organically enriched OMZs (Gooday et al. 2010). Other likely mechanisms that allow foraminifera to live in hypoxic and anoxic sediments have been reviewed by Koho and Piña-Ochoa (2012). They include the presence of bacterial endosymbionts (e.g., Bernhard 2003), the sequestration of chloroplasts (Bernhard and Bowser 1999; Grzyski et al. 2002), the proliferation of peroxisomes and mitochondria (Bernhard and Bowser 2008), and most notably, the respiration of stored nitrates (Risgaard-Petersen et al. 2006; Piña-Ochoa et al. 2010a, b). Denitrification as an alternative metabolic pathway, together with other physiological and ultrastructural adaptations, make foraminifera an important ecological group in oxygen-depleted environments (e.g., Woulds et al. 2007; Gooday et al. 2009a, b; Glock et al. 2012; Koho and Piña-Ochoa 2012; Mallon et al. 2012; Fontanier et al. 2014).

Response to changes in sea level and primary productivity

Rising sea level, by amplifying beach slopes, leads to increased wave exposure and favours the presence of coarser particles in intertidal ecosystems. This causes declines in the abundance of meiofauna and macrofauna, with potential adverse consequences for ecosystem functioning (Yamanaka et al. 2010).

Global warming is likely to have a widespread impact on the benthos through its effect on surface primary productivity, which depends on temperature, depth of the mixing layer, pH, oxygen concentrations and phytoplankton taxa (Wigham et al. 2003; Edwards and Anthony 2004). Deep-sea meiofauna play important roles in the processing and redistribution of food reaching the abyssal seafloor (Rex and Etter 2010). A reduction in the delivery of food to the seafloor linked to warming is likely to lead to reductions in body size, a trend that would favour the meiofauna at the expense of larger size classes (Smith et al. 2008).

Response to increased episodic events

Global change may also modify the cyclical pattern of climate turbulence, for example, the seasonal ‘El Niño’ event (Collins et al. 2010). El Niño has led to increased oxygenation of the central Chilean shelf, an area associated with an OMZ, as well as an increase in the supply of organic matter (Neira et al. 2001; Levin 2003). The 1997–1998 El Niño events caused changes in meiofaunal community in an upwelling region off Central Chile: harpacticoid copepod densities were nine times higher than during the previous year, but total meiofaunal densities were 42 % lower (Neira et al. 2001).

Climate change is also expected to increase the intensity and frequency of episodic events in mid-latitude regions of the

world (i.e., Mediterranean Sea; Somot et al. 2006; Coma et al. 2009). An example of such events is the dense shelf water cascading (DSWC), particular buoyancy-driven currents causing dense water to rapidly sink into deep basins due to the excess density gained by cooling, evaporation and freezing in the surface layer (Shapiro et al. 2003). A recent study in the Gulf of Lions (Pusceddu et al. 2013) reported that the 2005 DSWC event resulted in lower abundance, biomass and richness of all meiofaunal groups compared with other periods (Pusceddu et al. 2013).

Response to ice-shelf modifications

Global warming may lead to major changes in polar regions with regard to seasonal changes (ice-cover for example) that may directly affect meiofauna (Kramer et al. 2011). Change in climate is expected to form brackish and saline melt ponds that may provide new habitats for sympagic meiofauna (Jones et al. 2013). On the other hand, the melting of polar glaciers and the resulting glacial melt-water and fine sediments will lead to greater water-column turbidity, affecting phytoplankton production, and increasing sedimentation rates and burial disturbance in coastal regions, particularly fjords (W sławski et al. 2011). Global warming is also responsible for ice-shelf collapse around the Antarctic Peninsula (Scambos et al. 2003). Raes et al. (2010) investigated the effect of this phenomenon on Antarctic meiobenthos. Sea-ice collapse in Larsen continental shelf was associated with a phytoplankton bloom that affected pelagic organisms as well as meiofauna (Gutt et al. 2011), promoting the abundance and diversity of nematodes (Raes et al. 2010). A recent study of Rose et al. (2014) compared meiofauna from Larsen continental shelf stations with food-limited deep-sea stations in the Western Weddell Sea, and showed that meiobenthic communities have not yet recovered from the food-limiting conditions present at the time of iceshelf coverage. In recently ice-free areas close to a glacier in the West Antarctic Peninsula, meiofauna showed relatively low densities. However, the pioneer nematode genus *Microlaimus* reached high abundance in these newly exposed sites (Pasotti et al. 2014).

However, the largest global warming event will be when the opening Arctic creates polynyas into the open Atlantic Ocean. The New East Water polynya (NEW polynya) has become larger and larger, now reaching 43,000 km². The whole climate in Northern Europe strongly depends on Arctic polynyas. If both the North East Water polynya (NOW polynya) and NEW polynya collapse, it will affect the Gulf Stream. The unique meiofauna associated with NEW polynya will be endangered, risking extinction (see Huys et al. 1997; Worsaae and Kristensen 2003). The structure of meiofaunal communities inside the unique ikaite tufa columns in the Ikka Fjord is also endangered. These columns are formed by the rare mineral ikaite (calcium carbonate hexahydrate, see Buchardt et al.

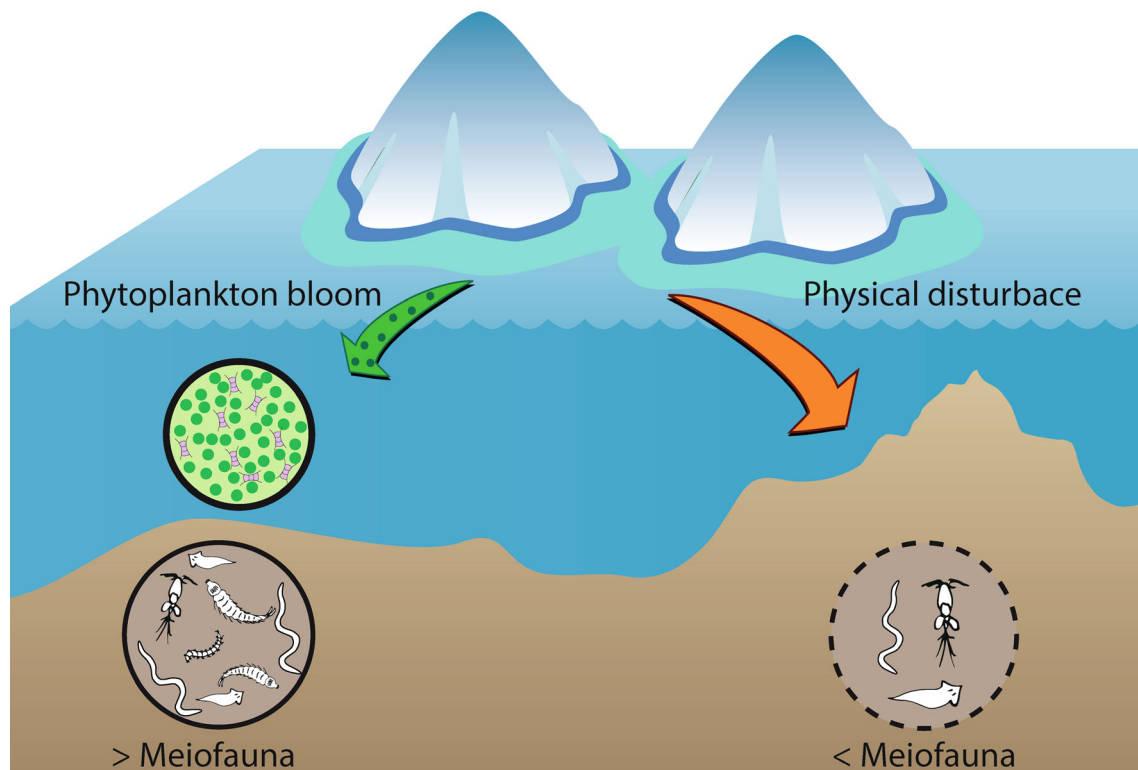


Fig. 2 Diagram of ice-shelf modification impacts on marine meiofauna

1997). The mineral ikaite is metastable, and the ikaite columns are already melting at a temperature of 6 °C (Buchardt et al. 1997). Meiofauna organisms are found both inside and outside the columns. In particular, a species-rich meiofauna community was described in the Atoll depression, including rotifers, kinorhynchs and eutardigrades (*Halobiotus crispae*), as well as new species such as the rotifer *Notholca ikaitophila* (Sørensen and Kristensen, 2000). The ikaite is only stable in water below 6 °C and the rising temperature is at risk of disintegrating the Ikka fjord and consequently its unique meiofauna community. A diagram of ice-shelf modification impacts on marine meiofauna is given in Fig. 2.

Meiofaunal organisms as useful test case of climate change studies

Experimental and modelling approaches are used to identify and predict ecosystem level changes in response to climate change (Wernberg et al. 2011). Regarding climate change effects in Antarctica, Ingels et al. (2012) provided a data synthesis on five important benthic taxa (Nematoda, Foraminifera, Isopoda, Amphipoda, Echinoidea). This study shows that foraminifers, in particular species with calcareous tests, are likely to be negatively impacted by ocean acidification, while nematode abundance may be stimulated by high concentrations of CO₂ and low O₂. Data on benthic macrofauna and

meiofaunal nematode diversity from the shelf margin of the North Pole suggest that both local (α -) and turnover (β -) diversity may be determined by ecological conditions (reported as food supply, sediment properties, disturbance, flow and bottom-water oxygen content; Renaud et al. 2006).

Some meiofauna groups, such as foraminifers and ostracods, can be very useful to the study of past climate change by the recovery of their fossil shell. For an exhaustive review on this matter, please refer to paleoclimatology studies. Benthic foraminifera, particularly species with calcareous tests, have a superb fossil record and are widely used by micropaleontologists to reconstruct conditions in the historical and geological pasts (Gooday 2003; Jorissen et al. 2007; Gooday et al. 2009a; Schönfeld et al. 2012). Their utility in palaeoceanography and palaeoecology is based on a considerable body of available knowledge regarding the adaptation of different species to particular environmental conditions (e.g., Murray 2006). The abundance, rapid reproductive rate and ecological sensitivity of species to different environmental conditions also makes foraminifera excellent candidates for monitoring the status of modern ecosystems, particularly those exposed to human impacts (Alve 1995; Mojtahid et al. 2008; Schönfeld et al. 2012). It is also possible to use foraminifera to reconstruct environmental baseline conditions prior to a disturbance event retrospectively (Gooday et al. 2009a). Bouchet et al. (2012) analysed benthic foraminiferan diversity

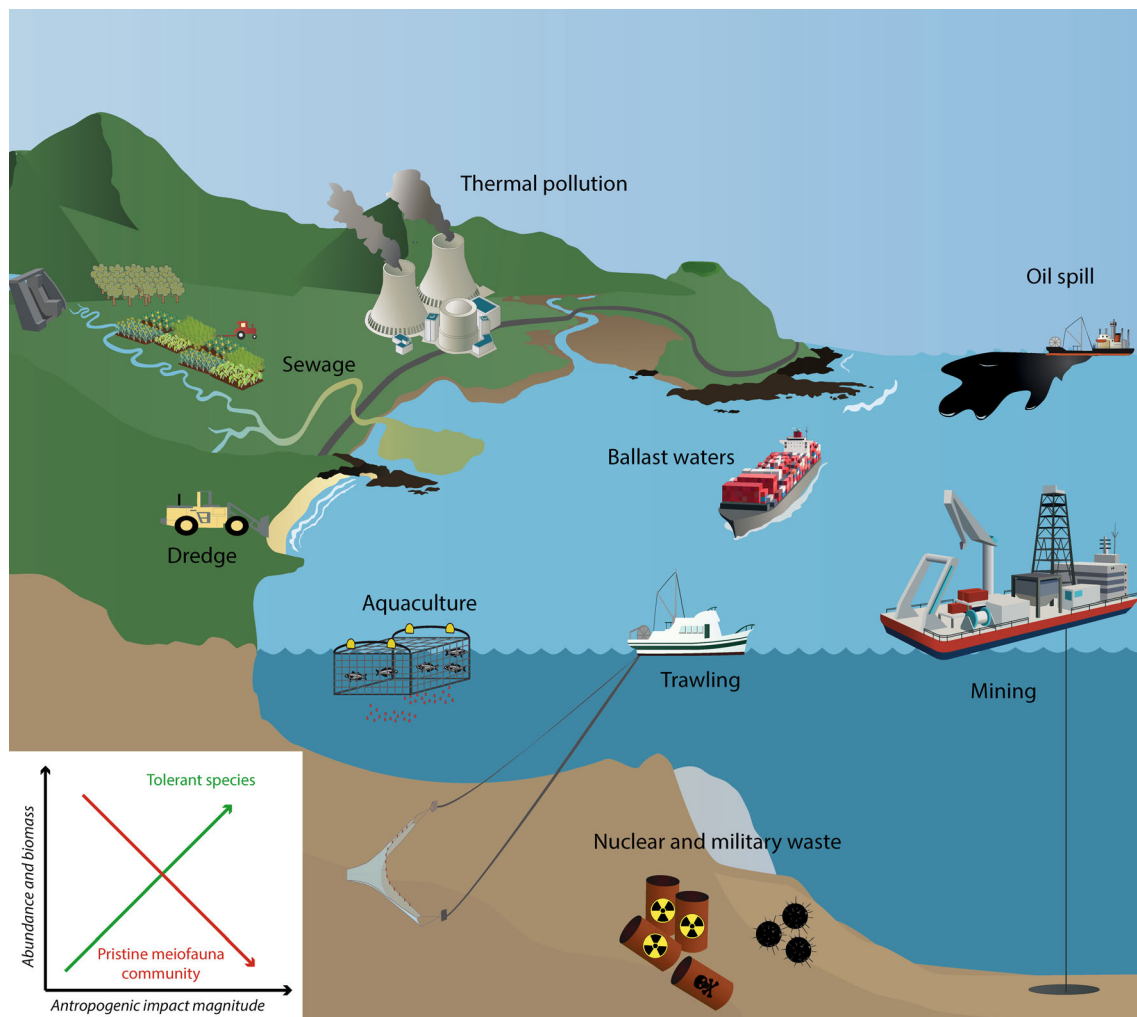


Fig. 3 Diagram of anthropogenic impacts on marine meiofauna

in the top 1-cm layer of sediments with respect to a bottom water oxygen gradient on the Norwegian Skagerrak coast, and established a clear pattern of “bad” to “high” Ecological Quality status (EcoQs). The correlation between bottom-water oxygenation and foraminiferal diversity suggests that benthic foraminiferal represent an efficient bio-monitoring tool to evaluate the EcoQS, a result already evident from OMZs studies (Goody et al. 2000, 2009b). The Ostracoda fossil record is of greatest value for tracing palaeo-climate events, providing valuable information on past water salinity, temperature and chemistry, hydrodynamic conditions, substrate characteristics, climate, sea level variations, oxygen and nutrient availability (Frenzel and Boomer 2005) and anthropogenic influences (Irizuki et al. 2015). Yasuhara et al. (2012a, 2014) used ostracod and foraminiferal fossil records from the last 250,000 years on the Shatsky Rise in the North Pacific Ocean to demonstrate that rapid climate changes affect deep-sea benthic diversity. They observed glacial-interglacial shifts in overall abundances and species diversities for both meiofauna taxa. Ruiz et al. (2004) described the recent

evolution of the Odiel Estuary (SW Spain) during the past decades and the influence of natural and anthropogenic factors analysing the distribution of Ostracoda and Foraminifera.

Richmond et al. (2007) modelled the effects of environmental variability on copepods using a 98-year salinity record for coastal South Carolina. This study showed that a greater frequency and magnitude of extreme events, such as precipitation and estuarine salinity reduction, negatively affect copepod population growth rates, with possible population declines. Since they represent an important food source for higher trophic levels, the reduction of the harpacticoid population may affect many other estuarine species, as well as species from other habitats whose larval stages develop in the estuary (Richmond et al. 2007).

Other anthropogenic impacts

It has been demonstrated that meiofauna, including foraminifera, are good indicators of the health of coastal marine

ecosystems (Vassallo et al. 2006; Balsamo et al. 2012; Schönfeld et al. 2012; Moens et al. 2014). In recent decades, a growing body of scientific literature has been dedicated to the response of meiofauna to anthropogenic impacts, such as pollution (Coull and Chandler 1992; Fleeger and Carman 2011; Balsamo et al. 2012; Moens et al. 2014). Meiofauna reflect changes derived from environmental disturbance, both spatially and temporally (Moreno et al. 2008), and can be considered a collective indicator of environmental quality since they display specific responses to different types of anthropogenic disturbance (Schratzberger and Warwick 1999; Danovaro et al. 2004b). Furthermore, the study of meiofauna is cost-effective compared with that of other benthic components (Rogers et al. 2008). These advantages favour the use of meiofauna as bioindicators, especially when the disturbance source has not been identified (Kennedy and Jacoby 1999). The diversity and richness of taxa are generally lower in polluted and stressed environments, due to the disappearance of more sensitive groups (e.g., ostracods, gastrotrichs, hydrozoans, tardigrades), leaving an assemblage dominated by tolerant organisms, such as nematodes (Pusceddu et al. 2007). The nematode/copepod ratio can be used as a tool to monitor organic pollution (Raffaelli and Mason 1981; Sandulli and De Nicola 1989) in intertidal and subtidal studies (Warwick 1981a; Amjad and Gray 1983; Sheills and Anderson 1985). For example, this biomonitoring index was applied in sediments affected by aquaculture wastes (Sutherland et al. 2007; Riera et al. 2011, 2012). The debate about the difficulty in the interpretation of this index (Coull et al. 1981; Lamshead 1984) was recently resolved by Sun et al. (2015). The incorporation of this index with environmental variables gives reliable information about anthropogenic disturbances (Sun et al. 2015). Alve (1995) provides a thorough review of the effects of different forms of pollution on benthic foraminifera. Thus, the “FORAM” (Foraminifera in Reef Assessment and Monitoring) Index (FI) assesses coral reef vitality and suitability of benthic environments for communities dominated by symbiotic algal organisms (Hallock et al. 2003). Ostracods respond to pollution-induced environmental changes showing high sensitivity to heavy-metal pollution, oil discharges and anoxic conditions (Ruiz et al. 2005). Some ostracod species are adapted to hypoxic conditions and can dominate in polluted environments (Alvarez Zarikian et al. 2000; Yasuhara et al. 2012b). In addition to changes in the Ostracoda community, morphological and geochemical changes can also be detected in ostracod shells (Ruiz et al. 2005). A schematic representation of anthropogenic impacts on marine meiofauna is illustrated in Fig. 3.

Trawling and other physical disturbances

Industrial fishing using bottom trawling is one of the most severe human-derived disturbances to the seafloor (Watling

and Norse 1998), and results in a substantial level of mortality among benthic invertebrates (van Denderen et al. 2013). Larger organisms, such as bivalves and crustaceans, suffer high mortality with long recovery times (Kaiser et al. 2006), whereas smaller meiofaunal taxa appear to have higher resilience to these disturbances (Jennings et al. 2001). Most studies have focused on megafauna and macrofauna, and relatively little is known about the impact of bottom trawling on meiofaunal communities (Moens et al. 2014). In general, meiofauna were less affected than macrofauna by physical disturbance, as in the case of sediment modifications due to the passage of large cruise liners (Warwick et al. 1990). For nematodes, trawling has been shown to have either a positive (Pranovi et al. 2000; Liu et al. 2009, 2011), negative (Schratzberger et al. 2002; Hinz et al. 2008) or minor impact on community structure (Schratzberger et al. 2002; Lampadariou et al. 2005). Nevertheless, a recent study showed that chronically trawled areas in the north-western Mediterranean Sea are characterised by significantly reduced meiofaunal abundance (80 %), biodiversity (50 %), and nematode species richness (25 %) when compared with non-trawled areas (Pusceddu et al. 2014a). However, a mesocosm experiment suggests that removal or reduced densities of larger macrofauna species as a result of trawling may lead to increased nematode abundance (Ingels et al. 2014). Environmental setting is, once again, a very important factor to be considered in impact studies, as demonstrated by a series of microcosm experiments designed to evaluate the effects of physical and biological disturbance and organic enrichment on nematodes (Schratzberger and Warwick 1998a, 1999). These experiments showed that nematodes inhabiting sand sediments suffered mainly when exposed to organic enrichment, while nematodes from mud sediments were more sensitive to physical disturbance (Schratzberger and Warwick 1998a, 1999).

Industrial discharge of hydrocarbon

Hydrocarbon pollution from maritime transport, offshore production, release of refined fuel or accidents can impact marine ecosystems (Arieli et al. 2011; Beyrem et al. 2010; Mahmoudi et al. 2005; Ernst et al. 2006). Hydrocarbons are composed of several types of molecules and can occur in solid, liquid or gaseous forms. These molecules change composition quickly within the first hours of release (Kingston 2002), due to factors such as photooxidation, sedimentation, evaporation and expansion of the oil slick (Ernst et al. 2006). Microbial degradation takes place and can be used as a tool for bioremediation (Schratzberger et al. 2003). Due to these chemical changes, the bioavailability of hydrocarbons may have different effects on benthic fauna, including meiofauna (Alve 1995). Foraminiferal organisms respond to hydrocarbon contaminations by an increase mortality rate and abnormality, and a decrease in density and diversity (Balsamo et al. 2012 and references

therein). After the sinking of the oil tanker *Erika* off the French coast, Ernst et al. (2006) studied the response of foraminifera to the presence of oil. Immediately after the accident, *Haynesina germanica* was the dominant species, but during the first 2 weeks, the authors observed a significant decrease in foraminiferal density compared with control sediments. After 4 weeks, a global density increase was observed, and after 4 months, new foraminiferal species, such as *Textularia earlandi* and *Ammonia* spp., dominated. Mahmoudi et al. (2005) added different concentrations of diesel oil to microcosms and compared the meiofaunal communities after 90 days. Nematodes showed a strong decrease in abundance and diversity. Some species, such as *Oncholaimus campylocercoides* and *Chaetonema* sp., declined, while others (e.g., *Marylynnia stekhoveni*) increased with higher diesel concentrations (Mahmoudi et al. 2005). Another controlled oil spill experiment in an intertidal zone was performed in a sandy beach of Korea (Kang et al. 2014). A dramatic impoverishment of meiofaunal abundance was detected during the first 4 days after the contamination, with slow recovery. One month after the contamination, meiofaunal communities recovered their pristine status (Kang et al. 2014).

A study by Montagna and collaborators (2013) investigated the impact of the Deepwater Horizon (DWH) accident in the northern Gulf of Mexico (April 2010, 1525 m water depth) on meiofauna. This study showed a severe reduction of meiofaunal diversity within 24 km² from the wellhead. Nematode abundance increased near the oil spill, while harpacticoid copepods decreased drastically, indicating a possible community-level trophic response due to the DWH-spill-enriched indigenous bacteria, which would be available as food for deep-sea nematodes (Montagna et al. 2013). Another study in the same area by Bik et al. (2012a) investigated meiofaunal communities prior to and following the oil spill and demonstrated significant changes in community structure, especially for nematodes. Prior to the spill, nematode genera exhibited high richness and evenness, whereas the post-spill communities consisted mainly of predatory and scavenger taxa. Similarly, nematode abundance and diversity significantly decreased with changes in taxonomic structure after contamination by polycyclic aromatic hydrocarbons (Louati et al. 2014). In contaminated sediments that had undergone treatment, biostimulation had a positive impact on community structure and diversity index, suggesting meiofauna as possible candidates for bioremediation of contaminated sediments (Louati et al. 2014). Considering available literature on nematodes affected by hydrocarbon contamination, variable responses have been reported (Balsamo et al. 2012 and references therein). These differences can be explained by different dosages, time of exposure, toxicity and bioavailability of hydrocarbons, together with the types of sediments and hydrodynamic conditions (Balsamo et al. 2012 and references

therein). All these parameters are to be taken in account in impact studies concerning meiofauna, and in particular, nematodes.

Thermal pollution

Hechtel et al. (1970) and Arieli et al. (2011) investigated the impact of thermal pollution on meiofauna due to water discharged from nuclear power plants. Hechtel et al. (1970) focused on benthic invertebrates from Long Beach (USA), reporting a decrease in species diversity and a change of dominant species. These observations reflect the disappearance of sensitive species at high temperatures. Arieli et al. (2011) investigated the impact of thermal pollution along a gradient at the outlet of the Central Hadera (Israel) power plant on foraminiferal communities. Temperatures exceeded 30 °C during the summer with a dramatic effect on populations, which showed a decrease in abundance and diversity. Species such as *T. agglutinans* were not present at polluted sites, while *Lachlanella* sp. tolerated high temperatures. The biology of nematodes found in percolating filter-bed sewage treatment plants was investigated by Woombs and Laybournparry (1984a, b). Temperature profoundly affected their feeding activity, ingestion rates, growth, reproduction and longevity. As temperature increased, the ingestion rates increased, while longevity decreased with higher temperatures.

Agriculture discharges and sewage

The increased use of fertilizer in agriculture has resulted in greater export of nutrients to the marine environment. These discharges can have various effects, and may, for instance, trigger green algal blooms that affect marine ecosystems. Algal blooms have a marked influence on the meiobenthos (Garcia and Johnstone 2006) following the deposition of fluffy layers of phytodetritus on the seafloor. These unconsolidated organic deposits, often agglutinated by mucous secretions, enhance microbial activity after relatively short periods (days to weeks), and can subsequently cause a significant increase in meiofaunal abundance and diversity (Giere 2009). Garcia and Johnstone (2006) investigated the impact of filamentous cyanobacterium *Lyngbya majuscula* blooms on the meiobenthos. A bloom led to oxygen depletion in sediments, causing a decrease in abundance and in their sediment depth distribution. However, the bloom did not affect the abundance and distribution of polychaetes as strongly as it did for copepods and nematodes. Green algae in the genus *Enteromorpha* are the main cause of the formation of reduced surface sediments or “black spots” on the tidal flats of the Wadden Sea (The Netherlands) (Neira and Rackemann 1996), leading to severe reductions of meiofaunal abundance and diversity (Neira and Rackemann 1996; Carriço et al.

2013). In an investigation of the impact of green tides on meiofauna on the Brittany coasts, a reduction in diversity and differences in species composition were recorded when comparing impacted and unimpacted beaches (Carriço et al. 2013). Similarly, in the Venice Lagoon (Italy), the communities at sites affected by the green alga *Ulva rigida* were different from those found in unimpacted sites (Villano and Warwick 1995). Drifting macroalgal mats frequently accumulate during the summer on Baltic Sea beaches, inducing anoxic and sulphidic conditions and leading to changes in meiofaunal composition. In particular, the nematode assemblages under the mats are characterised by low diversity and are dominated by the deposit feeder *Sabatieria pulchra* (Wetzel et al. 2002). Field studies show shifts in community structure and lower diversity in sites affected by sewage pollution (Coull and Chandler 1992). Experimental studies showed that nematodes can tolerate osmotic stress, regulating their water content by changes in their cuticle (Forster 1998). Some nematode genera (such as *Daptonema*, *Sabatieria*, *Pontonema*, and genera of the family Linhomoeidae) are particularly abundant in organically enriched locations (e.g., Warwick and Robinson 2000; Armenteros et al. 2010). Copepods showed endocrine alterations while in contact with released anthropogenic chemicals such as insecticides (Dahl and Breitholtz 2008).

Heavy metal pollution

Heavy metals are naturally present in both terrestrial and marine soils. Among heavy metals, some, such as iron, are essential for biological processes (Wang et al. 2014). However, at higher concentrations, specific elements, including copper, zinc or lead, can be toxic (Baize 1997). The inputs of heavy metals in the marine environments are mainly due to industrial activities. Paint factories, steel mills and waste dumps are all anthropogenic sources of heavy metals (Hack et al. 2007). Several studies have shown a decrease in meiofaunal diversity due to heavy metal pollution in coastal systems (Austen and McEvoy 1997; Gyedu-Ababio and Baird 2006). Some species disappear; others can become dominant (Hack et al. 2007). Copper seems to have the greatest impact on the structure of freshwater benthic communities (Burton et al. 2001). Tolerance to metal pollutants has been shown to vary widely among nematode species (Moens et al. 2014 and references therein). A study about the impact of heavy metals on nematodes from the Swartkops Estuary (Port Elizabeth, South Africa) revealed that nematode community structure was significantly impacted, with dominance of *Monhystera* and *Theristus* coloniser genera in the most polluted sites (Gyedu-Ababio et al. 1999). Some species, such as *Enoplus communis*, show low tolerance to metals (Howell 1983), while others, such as *Diplolaimella dievengatensis* and *Halomonhystera disjuncta* nematodes (Vranken and Heip 1986; Vranken et al. 1991; Gyedu-Ababio and Baird 2006), as well as copepods (Burton

et al. 2001), can be tolerant to high levels of heavy metals. Nematodes can accumulate and tolerate higher levels of copper, cadmium, zinc and lead than other meiofaunal organisms (van der Wurff et al. 2007 and references therein). However, changes in nematode genetic diversity can be induced by sublethal concentrations of metals (Derycke et al. 2007), and sublethal effects can be detected by life-history parameters, such as fecundity and development times (Vranken et al. 1991). Nematodes mainly store heavy metals in their subcutaneous tissue (Howell 1983) and gastrointestinal tract (Harvey and Luoma 1985), but they can also accumulate heavy metals in their mucus (Riemann and Schrage 1978; Jensen 1987; Decho 1990). Offshore nematode communities appear to be more susceptible to metals than near-shore communities (Austen and McEvoy 1997). High levels of heavy metals potentially generate test deformities in benthic foraminifera and modify community structure (e.g., Alve 1995; Ruiz et al. 2004; Armynot du Châtelet et al. 2004; Ferraro et al. 2006; Le Cadre and Debenay 2006). In an experimental study, Alve and Olsgard (1999) found that foraminifera were able to colonise sediments that were severely contaminated with copper. At high (967–977 ppm) and very high (1761–2424 ppm) concentrations, their abundance decreased and equitability increased. However, there was no effect on overall species richness, and in contrast to previous studies, there was no evidence of increased test deformation (Alve and Olsgard 1999).

Aquaculture

Aquaculture (i.e., farming of aquatic organisms such as fish, molluscs, crustaceans and aquatic plants, etc.) has rapidly expanded during the last decades in response to the depletion of natural fish stocks by overfishing (Jackson 2001). Under the cages used in fish farming, organic matter accumulates continuously and in great quantities due to the sedimentation of fish wastes (faeces and uneaten food). The accumulation of inorganic material causes eutrophication, which can lead to the development of anoxic sediments (Newell 2004). Aquaculture leads to changes in sediment composition that can impact benthic communities. This enrichment decreases with increasing distance from the cage (Mazzola et al. 1999; Forchino et al. 2011). Several studies have examined the impact of aquaculture on meiofauna (Sutherland et al. 2007; Mirto et al. 2010; Netto and Valgas 2010; Mirto et al. 2012). The enriched habitats are characterised by high densities of meiofaunal opportunistic nematodes and copepods able to utilise a wide variety of food resources (Warwick 1987). In particular, bacterial feeder nematodes can contribute to enhance the rate of bacterial decomposition of the detritus (Warwick 1987). A microcosm experiment showed that an increasing amount of organic matter has a negative effect on nematode diversity. The same concentration of organic matter given in many small quantities had milder effects on community

structure than when administered in fewer but larger quantities (Schratzberger and Warwick 1998b). In Mediterranean Sea fish farms, a strong effect on meiofaunal density and diversity is observed in sediments under the cages (Mirto et al. 2012). The abundance of some groups (i.e., kinorhynchs) decreases significantly or even disappears in the sediments under the cages, while others (i.e., polychaetes) increase in sediment with higher organic matter content (Mirto et al. 2012). A decrease in the abundance of some meiofaunal groups under the cages was also observed in salmon farms in Canada (Sutherland et al. 2007), and in mussel farming in Brazil (Netto and Valgas 2010). In a North Adriatic (Mediterranean Sea) fish farm, a different copepod community, also characterised by low abundance, was observed in the sediments under the cages (Grego et al. 2009). Studies comparing intensive and semi-intensive farming showed that low intensity farming does not impact on meiofauna community (Danovaro et al. 2004b). A number of studies have also analysed foraminiferal assemblages influenced by organic enrichment from fish farms (e.g., Schafer et al. 1995; Angel et al. 2000; Vidović et al. 2009), as well as the recovery of assemblages after the farming activity ceased (Oron et al. 2014). High population densities are associated with zones that are less severely impacted. These dense populations are dominated by species typical of organically enriched habitats. Recently, Pawlowski et al. (2014) used a next-generation metabarcoding approach (DNA and RNA) to evaluate foraminiferal diversity responses to organic enrichment associated with fish farms. This study revealed high variation among foraminiferal communities collected in the vicinity of fish farms and at distant locations, with evidence for species richness decreasing at impacted sites, especially visible in the RNA data.

Dumping of dredged material

Dredging and dumping of dredged material are a result of increasing human activities in coastal areas. The dumping itself has consequences for the water column and the seabed. In the water column, the main effects concern changes in turbidity, which can initiate changes in primary production and the release of materials, such as contaminants and organic matter. Sediment inputs to the seabed can also lead to smothering of the fauna, and may initiate changes in bathymetry (Engler et al. 1991). Therefore, dredged material can represent a potential resource to create and/or improve intertidal habitats (i.e., beneficial use; Bolam et al. 2006). It can also initiate an influx of organisms from other regions, especially when the fauna in the dredging area is different from that of the dumping area (Van Hoey et al. 2011). In south-eastern England, 3 years after dredging, meiofaunal and macrofaunal communities rapidly recolonised sediments (Bolam et al. 2006). After 3 months, macrofaunal and meiofaunal assemblages were rich and diverse, despite the presence of sediments with physico-

chemical characteristics different from those found in surrounding areas (Bolam et al. 2006). This study also supported the hypothesis that meiofaunal recolonisation occurred primarily through the direct transfer of individuals, i.e., the settlement of a small number of meiofaunal organisms passively re-suspended in the discharged material. A study on the Belgian coast, comparing nematode communities after sand extraction and 2 years later, showed that nematode community composition was more stable after 2 years than at the extracted sites (Vanaverbeke and Vincx 2008).

Introduction of alien species

Ballast water discharges by ships can have a negative impact on marine ecosystems and also on meiofauna. *Ostreopsis ovata*, a dinoflagellate non-toxic epiphytic species commonly found in the tropics (Gallitelli et al. 2005), was introduced into Mediterranean Sea via ballast waters (Guidi-Guilvard et al. 2012). This species develops on the brown alga *Halopteris scoparia* under optimal conditions and becomes toxic (Guidi-Guilvard et al. 2012). Analyses showed that high concentrations of *O. ovata* are associated with changes in the community structure of the phytal meiofauna. Gollasch (2002) recorded non-native foraminiferal species transported in ballast tank sediments from ships sailing into German ports. Along the French Atlantic coast, Bouchet et al. (2007) documented the occurrence of *Quinqueloculina carinatastriata*, a foraminiferal species that was likely introduced from the Mediterranean and Red Seas by mariculture trade or shipping activities. The survival of tropical plankton organisms in ballast waters was studied by accompanying a container vessel on its 23-day voyage from Singapore to Bremerhaven in Germany (Gollasch et al. 2000). For two tanks, one filled off Singapore and the other off Colombo, Sri Lanka, their phytoplankton and zooplankton content was monitored with daily sampling. As reported in previous studies, species abundance and diversity, especially of zooplankton, decreased sharply during the first days, and only a few specimens survived the whole cruise. The contents of the Colombo tank, however, changed dramatically during the last week of sampling. The harpacticoid copepod, *Tisbe graciloides*, increased in abundance by a factor of 100 from 0.1 to 10 ind/L within a few days. This was the first time that a species found in ballast water multiplied at such a high rate. Opportunistic species such as *T. graciloides* are apparently able to thrive and propagate in ballast water tanks under certain conditions. Ballast water tanks may thus serve as incubators for certain species (Gollasch et al. 2000; Levings et al. 2004).

Munition and nuclear waste dump sites

Chemical munition dump sites are places where weapons and chemical munitions have been dumped. Since World War II,

thousands of tons of chemical munitions have been dumped into the Baltic Sea (Grzelak and Kotwicki 2014) where meiofaunal communities were poor, not only in terms of abundance, but also in terms of number of taxa (Kotwicki et al. submitted). At dumping sites associated with hypoxic and/or anoxic conditions, the communities are composed of well-adapted organisms and dominated by mud-dwelling nematodes like *Sabatieria*, *Terschellingia* and *Halomonhystera* species. *Halomonhystera disjuncta* showed ovoviviparous reproduction, which secures the survival of the broods (Grzelak and Kotwicki 2014). Sediment burial significantly reduces the toxicity of 2,4,6-trinitrotoluene (TNT) in marine ammunition dumping for the copepod *Nitocra spinipes*, especially in fine-grained sediment (Ek et al. 2007). There is still a remarkable lack of information on the environmental impact of radioactive waste that was disposed of in abyssal oceans in the second half of the 20th century (IAEA 1999). The Barents Sea represents one of the best-known nuclear-polluted marine zones; nuclear tests were carried out in this marine environment by the USSR and nuclear waste has also been dumped there (Galtsova et al. 2004). Pogrebov et al. (1997) showed that meiofaunal communities were different between control and radionuclide-polluted sites. A significant increase in meiofauna diversity was observed at higher concentrations of ^{137}Cs (Galtsova et al. 2004). Alexeev and Galtsova (2012) showed a positive correlation between radio-caesium concentrations and the taxonomic diversity of meiofauna. Furthermore, meiofauna react faster than the macrobenthos to radioactive pollution through changes in diversity and abundance; the macrobenthos is more stable and shows fewer effects in the short term (Alexeev and Galtsova 2012).

Exploitation of mineral resources

The exploitation of mineral resources has a direct impact on the benthic community due to removal of resources, and also an indirect impact made by shallow-water mining wastes. The effects of shallow-water mining wastes (heavy metals) on meiofauna were investigated in the Fal Estuary system (south-west England), revealing that some nematode species may have developed different tolerance mechanisms to survive in areas with high heavy metal concentrations (Somerfield et al. 1994). Microcosm and mesocosm scale experiments on meiofauna recolonisation in discharges tailing sediments were performed in Benete Bay (Indonesia; Gwyther et al. 2009). This study revealed that meiofauna colonised tailing sediments after 40 days and recovered control values after 97 days.

The deep-sea realm is one of the least-known oceanic areas on Earth, but this remote environment harbours large areas of concentrated metal reserves (Thurber et al. 2014). Many of these metals are used in electronics, and since terrestrial supplies are diminishing, deep-sea mineral resources are likely to be extensively mined within the next few decades (Thurber

et al. 2014). We are experiencing an increasing attention on exploration and mining of deep-sea minerals (such as cobalt-rich ferromanganese crusts, seafloor massive sulphide deposits and polymetallic nodules). In addition to the physical disturbance due to mineral deposit extraction, the reduction in habitat heterogeneity (Zeppilli et al. 2014) may permanently alter the structure of benthic communities (Leduc et al. 2015 and references therein). Benthic meiofauna from polymetallic nodule areas are known from the Pacific Ocean (Hessler and Jumars 1974; Snider et al. 1984; Renaud-Mornant and Gournault 1990; Bussau et al. 1995; Ahnert and Schriever 2001; Radziejewska 2002; Lambshead et al. 2003; Veillette et al. 2007a, b; Miljutin and Miljutina 2009a, b; Miljutina et al. 2010, 2011; Miljutina and Miljutin 2012) and Indian Ocean (Parulekar et al. 1982; Ansari 2000; Ingole et al. 2000, 2005; Singh et al. 2014). The techniques used for the extraction of nodules from the seafloor involve mechanical screening, bucket or scraper methods or hydraulic approaches to lift the nodules from the seafloor (Thiel 2003). These techniques can lead to the complete destruction of the upper 5–10 cm layer of soft sediments and the removal of nodules dispersed in the upper sediment layer (Miljutin et al. 2011), killing most meiobenthic organisms inhabiting the upper 0–5 cm layer of sediments, as well as those colonising the nodules. Chung et al. (2002) summarised the potential impact on benthic fauna during mining activities: (1) direct impact along the track of the nodule collector, where the sediment and associated fauna is crushed or dispersed in a plume, and the nodules are removed, (2) smothering or entombment of benthic fauna by the sediment plume, and (3) destruction of food resources for some species. The nodules themselves constitute a specific habitat for some organisms inhabiting their surface and the interstitial space inside their crevices and internal cavities (Thiel et al. 1993; Veillette et al. 2007a, b). In general, nematodes inhabiting the surface and crevices of nodules differ from the assemblages in the surrounding soft sediments, and some species are exclusively reported only in nodule crevices (Bussau 1993; Thiel et al. 1993; Bussau et al. 1995; Veillette et al. 2007a, b). Surprisingly, Bussau (1992) also found unique tardigrade fauna on and inside the manganese nodules from the Peru Basin at water depths from 4140 to 4170 m. The new genus and three new species he described (Bussau 1992) have never been observed outside the manganese nodule area and may be endemic. However, unless more sampling is undertaken, it cannot be concluded if this is a question of pseudo-endemism due to undersampling or if these species are truly endemic to the manganese nodule field, and in this case, if the nodule-associated fauna will also be lost during mining. Experiments conducted on the impacts of nodule mining on abyssal nematode communities in the Clarion-Clipperton Fracture Zone (Tropical and Equatorial Pacific) showed a negative impact on nematode abundance and diversity (Vopel and Thiel 2001). The severity of the impact was demonstrated by

changes in meiobenthic abundance, presence/absence of key taxa, and species diversity for nematodes and harpacticoid copepods (Radziejewska 2014). The impact remained detectable 26 years after the initial disturbance (Miljutin et al. 2011).

Conclusions and perspectives

The benthic fauna within an ecosystem have different body size spectra that reflect structural and functional aspects. Marine benthos forms an intricate network in which each group/species contributes functionally. This review demonstrates that meiofauna, besides being fundamental to understand the structure and functioning of marine communities, can be used as a proxy for responses of benthic communities to environmental changes.

This review shows that meiofauna can be a useful tool to investigate the impacts of climate change. In most studies, global change negatively impacts meiofaunal communities, which experience a reduction of abundance and diversity, with important consequences on benthic food webs. Overall, meiofauna are less negatively affected by climate change than are macrofauna; for example, at very low oxygen concentrations, only meiofaunal organisms survive. Some species of nematodes and foraminifers can even be favoured by the occurrence of extreme environmental conditions. The presence of these “extreme” species can be used as a warning signal of global change. Some climate impacts, such as ice-shelf modifications, can have opposite effects on meiofauna: negative (by increasing physical disturbances on the seafloor) and/or positive (by creating new habitats and promoting phytoplanktonic blooms). In any case, unique meiofaunal communities such as those found on the NEW polynya and in the Ikka Fjord, are endangered by ice-shelf modifications, with the risk of extinction.

Meiofauna are doubtlessly good indicators of anthropogenic impacts, and reflect spatial and temporal changes. However, it is difficult to correctly interpretate meiofaunal responses without information about abiotic factors. Therefore, measurements of associated environmental conditions are fundamental in the interpretation of the observed patterns. Considering environmental parameters together with meiofaunal indices strengthens scientific interpretations and provides useful tools for the detection of anthropogenic disturbances. Multistressor experiments are more informative than single stressor ones, revealing complex changes in ecological and biological interactions, and a precautionary approach may be required when interpreting single stressor studies. Anthropogenic pollutions generally have a negative effect on meiofauna. However, the increase in sea surface primary production and algal blooms generally has a positive effect on nematode abundance and biomass, and habitat formation such as dumping of dredged material may increase meiofaunal abundance and diversity by locally increasing heterogeneity. As in the case of climate, some species can tolerate

polluted conditions and show physiological changes. In addition, several meiofaunal species are specific to a kind of impact and can be used as detection tools. For organic enrichment, it was proved that the partitioning of organic inputs (as for aquaculture) can significantly reduce the impacts on meiofauna. In some ecosystems, the recovery time for the meiobenthic community can be very slow, as in the case of the deep-sea exploitation of minerals where severe habitat destruction may induce a loss of biodiversity over several decades.

Four taxonomic groups are valuable for predicting global changes: foraminifers (especially calcareous forms), nematodes, copepods and ostracods. Foraminifers and copepods are very sensitive to changing environmental conditions, while some nematode species are particularly tolerant to stress. Further studies about global change impact on less represented taxa are thus necessary.

In summary, compared to other benthic groups, meiofauna can be particularly valuable in impact studies. The study of meiofauna is cost-effective compared to that of other benthic components, and their use as bioindicators is particularly useful when the source of disturbance has not been identified, and to identify the effects of different forms of ecosystem perturbations. Nevertheless, meiofaunal taxonomic identification remains a challenge and a lack of experts complicates the task. Identification can be facilitated by using free computer-based illustrated keys that are accessible online (e.g., NEMYS <http://nemys.ugent.be/> for nematodes; <http://copepodes.obs-banyuls.fr/en> for copepods; Ellis and Messina <http://www.micropress.org/em/about.php> and World Foraminifera Database <http://www.marinespecies.org/foraminifera/> for foraminifera). The development of molecular approaches is bringing significant help to reinforce taxonomic identification and to distinguish morphologically similar species and cryptic species. These also include the development of rapid molecular methods for the identification “en masse” of small metazoans (Bik et al. 2012b), such as high-throughput next-generation sequencing (Fonseca et al. 2010) and proteomic fingerprinting (Laakmann et al. 2013). This review has elucidated the importance of meiofauna in global change impact studies. There is an urgent need to focus impact research on the taxonomy, genetics and function of keystone meiofaunal taxa or species.

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Glossary

Bleaching	Expulsion of the endosymbiotic algae (zooxanthellae) or their algal pigment from the tissue of symbiotic invertebrates (mainly reef corals), which lose their colour and turn white. Coral can survive a bleaching event, and at times it may be a reversible process, depending on the intensity and extent of the phenomenon. Several factors can cause the bleaching (e.g., increased or decreased light, thermal stress, bacterial infections).
Deposit feeder	An animal that ingests deposited, particulate material that primarily consists of inert sediments of low food value (mineral grains, refractory organic matter, etc.).
Ecosystem functions/ Ecosystem functioning	The sum of biological, geochemical, and physical processes that operate within an ecosystem, sustaining the overall performance of the ecosystem and supplying ecosystem services.
Idiosyncratic model	The idiosyncratic model suggests that the relationship between species richness and ecosystem functioning results in an extremely variable ecosystem. More specifically, the idiosyncratic relationship implies that each species has a different contribution to ecosystem functioning, depending on its interspecific interactions.

Macrofauna	Benthic animals retained on a 1-mm sieve.
Meiofauna	Benthic animals passing through a 1-mm sieve and retained on a 20- μ m sieve.
Permanent meiofauna	Organisms that spend their entire life cycle in the meiofauna size category.
Phytal meiofauna	Meiofauna living in close association with seagrasses, kelp and seaweeds.
Rivet model	The rivet model is based on the potential overlap and complementarity among the functions of different species. In this model, when a species is removed or added to an ecosystem, its contribution to ecosystem functioning is relatively small. This allows the system to keep the ecological function when a few species are lost.
Sympagic meiofauna	Meiofauna living in close association with sea ice, either on the ice under-surface, on the soft lower ice layer, within briny channels or pockets in the solid sea ice, or at the interface with water below the sea ice.
Temporary meiofauna	Organisms that are part of the meiobenthos only during a stage of their life (i.e., larvae and juveniles stages of macrofauna).

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